

SEASONAL PLASTICITY IN FAUNAL DIETARY STATUS, DIVERSITY AND FORAGING PERFORMANCE OF *ILISHA AFRICANA* (CLUPEIDAE) IN Qua IBOE ESTUARY, NIGERIA

by

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ABSTRACT. - The faunal dietary composition of *Ilisha africana* (Bloch, 1795) in Qua Iboe estuary, Nigeria, comprised primarily mysids and decapod crustaceans while fish eggs were of secondary importance. Other dietaries (amphipods, clupeids, unidentified fish, fish larvae, cephalopods, polychaetes, nematodes) were of incidental importance. Overall food richness and diversity (B_n) were low, depicting that *I. africana* is an oligophagous carnivore; this feeding regime was maintained throughout the dry (November-February) and wet (March-October) seasons in spite of slight short-term (month-to-month) variations. There was a positive relationship between reproductive investment and B_n whereas fat index (FI) decreased with increase in B_n . Diet diversity was higher in the dry season than during the rains; this conformed to the optimal foraging theory when viewed vis-a-vis the cycle in food resources availability and abundances in tropical aquatic systems. Foraging performance (FP) was higher in the wet season than during the dry season. It was inversely related to B_n but positively to FI. The seasonality in FP was linked with the breeding cycle of the fish.

RÉSUMÉ. - Le régime alimentaire de *Ilisha africana* (Bloch, 1795) dans l'estuaire de la Qua Iboe, au Nigéria, est surtout composé de mysidacés et de crustacés décapodes tandis que les oeufs de poissons sont de moindre importance. Les autres proies (amphipodes, clupéidés, poissons non identifiés, larves de poissons, céphalopodes, polychètes et nématodes) sont accessoires. Dans l'ensemble, la richesse et la diversité de la nourriture (B_n) sont limitées, ce qui montre que *I. africana* est un carnivore oligophage. Ce régime alimentaire est maintenu pendant les saisons sèche (novembre-février) et humide (mars-octobre) malgré de légères variations d'un mois à l'autre. Il existe une relation positive entre l'investissement reproducteur et B_n , tandis que l'indice de poids (FI) diminue lorsque B_n augmente. La diversité du régime est plus importante pendant la saison sèche que pendant la saison des pluies; cela est conforme à la théorie de l'optimisation de l'utilisation de l'apport nutritif vis-à-vis du cycle de la disponibilité des ressources alimentaires et des abondances dans les systèmes aquatiques tropicaux. La performance d'utilisation des aliments (FP) est plus importante pendant la saison humide que pendant la saison sèche. Ceci est inversement lié à B_n mais positivement lié à FI. La saisonnalité de FP est liée au cycle reproducteur du poisson.

Key-words. - Clupeidae, *Ilisha africana*, Nigeria, Diet diversity, Foraging success, Fat index, Reproductive investment, Seasonality.

Animal ecologists have established a strong functional relationship between foraging performance and reproductive success of several species (Dajoz, 1977; Angermeier, 1982, 1985). This arises from the fact that the amount of food consumed influences the magnitude of relative reproductive energy allocation; moreover, the quality and quantity of food consumed are known to affect growth rate, longevity, sexual maturity and fecundity of animals (Dajoz, 1977). In fishes, increased amount of available

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food results in accelerated growth rate and attainment of sexual maturity, increased fecundity, number of fertile eggs laid, visceral fat deposits and juvenile survival (Nikolsky, 1963; Wootton, 1973; Bagenal, 1978). Therefore in any aquatic ecosystem, the evolutionary adaptations should be associated with a natural selection pressure that favours fish species that have developed strategies for the optimization of foraging performance.

The diversity of items consumed by fishes (measure of dietary complexity or specialization: King, 1989) varies considerably among species; some are highly specialized or oligophagous, utilizing a limited number of food resources while others are polyphagous, subsisting on a wider array of items. The adaptative significance of the evolution of a broad trophic spectrum (high diet diversity) is that it ensures a constant energy source, facilitates adequate utilization of available food resources and enables the fish to easily switch from one food source to another in response to natural fluctuations in their relative abundances and availability (King, 1989).

Tropical fishes exhibit broad life history responses to the varying seasonality regimes prevailing in the various aquatic ecosystems. Seasonality in habitat conditions affect fishes mainly through qualitative and quantitative changes in available food resources (Lowe-McConnel, 1987). Temporal variations in diet diversity and foraging performance presumably educe from the inherent dynamics in food resources abundances / availability and/or changes in the species' foraging behaviour (e.g., active predilection for specific food-types) which may be mediated by the reproductive state of the fish (King, 1991). Therefore, a study of the temporal patterns in diet diversity and foraging performance may elicit information that is crucial in understanding the life history strategy of a fish species.

The present study was intended to document the overall faunal diet composition and the extent of temporal (monthly and seasonal) plasticity in the diet composition, diet diversity and foraging performance of the commercially important clupeid, *Ilisha africana* (Bloch, 1795) in the Qua Iboe estuary, Nigeria; it centres on the influence of the dry-wet season cycle on the seasonality regimes of these trophic attributes. The results are discussed in the light of the framework of the reproductive strategy of the fish (King, 1991) and the functional relationship between foraging performance and diet diversity.

Study area

The Qua Iboe estuary (Fig. 1) is the main outlet of the discharges of Qua Iboe river ($7^{\circ}30' - 8^{\circ}20'W$; $4^{\circ}30' - 5^{\circ}30'N$) which is the dominant hydrographic feature in Akwa Ibom State, Nigeria. It is situated in the rainforest belt of the southeastern coast of the country in the Bight of Bonny. The estuary comprises tidal creeks, small brackish water lagoons and a narrow fringe of mangrove swamp.

The vegetation of the mangrove swamp forest consists predominantly of *Rhizophora harrisonii*, *R. mangle*, *R. racemosa*, *Avicennia africana* and *Laguncularia racemosa*; other macrophytes include *Elaeis guineensis*, *Nypa fruticans*, *Phoenix reclinata* and *Achrosticum aureum*. The mangrove swamp forest is backed by a dense strip of an admixture of primary and secondary forests.

The estuarine climate of Qua Iboe river is typical of the hot-humid equatorial rainforest regime characterized by year-round precipitation. Nevertheless, two main seasons (dry and wet) are discerned in the area; the dry season extends from November to February with peak in January. During the dry season, dry north-east winds blow from the Sahara desert. The wet season ranges between March and October, with peak in August; it is typified by the prevalence of rain-bearing south-west winds blowing onshore from the Gulf of Guinea.

Within the last two decades, the Qua Iboe estuary has been subjected to considerable anthropogenic perturbations resulting from crude oil exploitation (Oladimeji, 1987; pers. obs.). Several episodes of varying levels of crude oil pollution are consequently commonplace in the estuary.

MATERIALS AND METHODS

This investigation was conducted over a 12-month span, ranging from November, 1987 to October, 1988 inclusive. During the sampling day of each month, specimens of *Ilisha africana* (Bloch, 1795) were collected (at about noon) from artisanal fishermen who landed their catch at Ibeno terminal (Fig. 1). Fishing was mainly done by the use of encircling gill-nets (50-70 mm stretched mesh) operated from dug-out canoes (7-12 m overall length) some of which were powered by 15 - 40 HP outboard motors.

The specimens were transported to the laboratory where they were measured to the nearest 0.1 cm total length (TL); they were frozen for 2 - 5 days pending further examination. Specimens were later eviscerated and the stomachs slit open. Only non-empty stomachs of fish ≥ 11.0 cm TL were used for analyses of the faunal diet composition, diet diversity and foraging performance. This was intended to avoid possible ontogenetic effects of smaller fish which were not equally represented in all monthly samples. A previous study (King *et al.*, 1991) has demonstrated that animal items form the bulk of the food of *Ilisha africana* in the Qua Iboe estuary.

The stomach contents of each specimen were placed in a petri dish and aggregates dispersed with a few drops of water prior to macroscopic and microscopic ($\times 40$) examination. The contents were sorted, identified and the relative importance of the components were numerically assessed. In this method, the number of individuals of each prey-type (fish eggs inclusive) in all the stomachs was expressed as a percentage of the total number of prey-types (Hyslop, 1980). Items with ≥ 10 % contribution to food composition were arbitrarily considered as primary foods; those with 1.0 - 9.9 % composition as

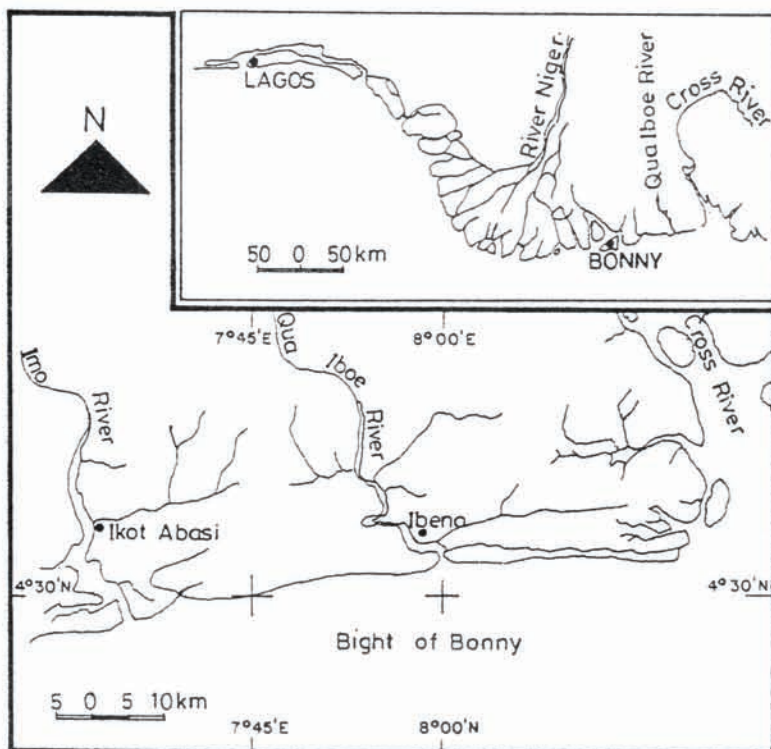


Fig. 1. - Map of southeastern coast of Nigeria showing the Qua Iboe estuary. Inset: the coast of Nigeria showing the Qua Iboe river.

secondary and those with < 1.0% composition as incidental dietaries. The non-faunal food items encountered were noted and the frequency of occurrence of each calculated (the number of stomachs in which each item occurred expressed as a percentage of total number of stomachs examined: Hyslop, 1980).

Unadjusted food richness (UFR) was considered as the total number of items recorded in the diet (King, 1989) while adjusted food richness (AFR) was estimated from Margalef's variety index (Odum, 1971) to compensate for the varying number of stomachs examined. Diet diversity was estimated from the percentage numerical composition data, using the index B_n (Angermeier, 1982):

$$B_n = [(1 / \sum_{i=1}^n P_i^2) - 1] / (n - 1) \quad (1)$$

where n = number of food categories in the diet and P_i = proportion of the diet comprised by resource type i . This index combines two attributes, food richness and evenness (the degree to which all items are equally represented); it increases as food richness or its evenness increases and declines when few items dominate the diet. B_n is scaled such that 1.0 represents an even distribution and zero, a strongly skewed distribution. Between-month and season diet overlaps were evaluated using the percentage similarity coefficient S (Moss and Eaton, 1966):

$$S = \sum_{i=1}^n \min. (X_i, Y_i) \quad (2)$$

where X_i and Y_i = proportions of the components of the series of n th item comprising the diets of X and Y . This index ranges from zero, for totally dissimilar dietary compositions, to 100% for identical diets.

The index of foraging performance (FP) was calculated as the number of prey (regardless of taxa) eaten per fish (Angermeier, 1982, 1985). In the present study, foraging success was assumed to increase with increase in FP.

The amount of visceral fat deposit in each specimen was estimated semi-quantitatively according to an arbitrary 0-20 points scheme (cf. Nikolsky, 1963); thus ratings of 0, 5, 10, 15 and 20 points were assigned to absence, scanty, light, moderate and heavy fat deposits respectively; intermediate points were also awarded in cases of intermediate amounts of fat. The fat index (FI) was then calculated as mean points per fish. Female gonadosomatic index (GSI) (weight of ovary relative to total body weight, expressed as a percentage) was used to depict patterns in reproductive investment.

RESULTS

A total of 517 specimens of *Ilisha africana* (11.3 - 21.1 cm TL) were examined. The monthly number of specimens examined ranged between 20 and 80; the dry season sample comprised 202 specimens (12.0 - 20.0 cm) while 315 specimens (11.3 - 21.1 cm) were examined during the rains.

Diet composition

The array of items in the composite diet of *Ilisha africana* (Table I) revealed that ten major faunal food-types were ingested, of which two (decapods and mysids) were primary dietaries, one (fish eggs) a secondary dietary while the remaining seven were of incidental importance. It fed predominantly on macrocrustaceans (95%) while fish, molluscs, annelids and nematodes were of minor importance, each accounting for < 5% of the diet.

Table I. - Gross trophic spectrum and seasonal variations in the relative importance of the dietaries of *Ilisha africana* in Qua Iboe estuary.

Food items	% Numerical composition		
	Overall	Dry season	Wet season
Crustaceans			
Eucarida: Decapoda	29.6	31.7	28.0
Pericarida: Mysidacea	65.1	60.5	68.6
Amphipoda	0.6	0.3	0.8
Fish			
Clupeids	0.1	0.1	0.2
Unidentified fish	0.8	1.3	0.6
Fish larvae	0.1	-	0.1
Fish eggs	3.2	6.0	1.1
Molluscs			
Cephalopoda: Teuthoidea	0.1	-	0.1
Annelids			
Polychaeta: Errantia	0.2	-	0.3
Nematoda (free living)	0.2	0.1	0.2
Total	100.0	100.0	100.0

Crustaceans consumed were dominated by mysids (mostly *Rhopalophthalmus africanus*) while the composite of penaeid (*Parapenaeopsis atlantica*) and palaemonid (*Nematopalaemon hastatus*) natant shrimps was subdominant; amphipods constituted only 0.6% of the diet. The clupeids recorded in the diet were mainly juveniles of *Ilisha africana* while other prey fishes (adults and larvae) eaten were already in advanced stages of digestion and were unidentifiable. A comparison of the fish eggs in the stomachs and ovaries of *I. africana* suggested that this fish preyed heavily on its own eggs. Cephalopods and polychaetes consumed were represented by *Sepia* and *Nereis* respectively.

Non-faunal materials encountered in the stomachs but precluded from analyses of diet diversity and foraging performance comprised sand grains (4.8% occurrence), detritus (0.5%) and algal fragments (mostly *Dinobryon*: 0.1%); these items appeared to have been inadvertently ingested and occurred in non-discrete units in the stomachs examined.

The monthly dynamics in diet composition (Table II) showed that the food-types can be arranged in two groups according to their monthly occurrences: group 1 consists of five items (decapods, mysids, amphipods, unidentified fish, fish eggs) which consistently occurred in 7 - 12 months of the year; group 2 comprises the remaining five items (clupeids, fish larvae, cephalopods, polychaetes, nematodes) which were encountered in < 5 months of the year and may thus be regarded as accessory dietaries. Decapods were of primary importance in November-February and June-October while in March-April, they were secondary dietaries. Mysids dominated the diet in all months except February and June when they were replaced by decapods and amphipods respectively. Mysids accounted for 50.7 - 92.6% of the diet in November-January, March-May and July-October whereas lower proportions (8.8 - 42.1%) occurred in December, February and June. A comparison of the dynamics in fat reserves (Fig. 2c) and diet com-

Table II. - Monthly variations in the % numerical composition of the dietaries of *Ilisha africana* in Qua Iboe estuary.

Food items	Months											
	N	D	J	F	M	A	M	J	J	A	S	O
Decapoda	29.9	16.7	34.6	40.6	1.7	4.7	-	20.6	34.7	36.1	26.9	47.4
Mysidacea	68.7	42.1	60.7	22.9	92.6	89.2	80.0	8.8	60.4	60.6	72.6	50.7
Amphipoda	0.4	-	0.1	1.4	-	0.7	12.0	44.1	0.8	-	-	-
Clupeids	-	-	-	0.7	-	-	-	-	0.6	0.5	0.1	-
Unidentified fish	0.3	7.9	0.7	4.7	0.6	-	-	-	1.8	0.5	0.3	-
Fish larvae	-	-	-	-	-	-	-	-	0.2	0.5	-	-
Fish eggs	0.7	33.3	3.7	29.7	5.1	5.4	8.0	11.8	0.6	-	0.1	1.9
Cephalopoda	-	-	-	-	-	-	-	2.9	-	0.3	-	-
Polychaeta	-	-	-	-	-	-	-	11.8	0.9	-	-	-
Nematoda	-	-	0.2	-	-	-	-	-	-	1.5	-	-

position showed a positive correlation between fat index and the proportion of mysids ($r = 0.636$, $df = 10$, $P < 0.05$); this relationship is represented by the linear equation:

$$FI = 6.3188 + 0.0316 \% N (\text{mysids}) \quad (3)$$

Amphipods were of secondary and primary importance in February and May-June respectively while in November, January, April and July, they were consumed as incidental items.

Clupeids were of incidental importance in February and July-September and fish larvae, in July-August. Unidentified fish constituted secondary food items in December, February and July and incidental items in November, February, March and August-September. Fish eggs were primary dietaries in December, February and June and secondary dietaries in January, March-May and October; they were of incidental importance in November, July and September. The relative importance of cephalopods was of secondary and incidental statuses in June and August respectively and nematodes, in August and January respectively.

The overall diet data for the two seasons (Table I) revealed that fish larvae, cephalopods and polychaetes were not consumed during the dry season whereas the spectrum of items presented in table I, were contained in the wet season diet. The fish fed to a larger extent on decapods, unidentified fish and fish eggs in the dry season than during the rains while the proportion of mysids was higher during the rains than in the dry season.

Diet constancy

There was considerable variation in month-to-month diet compositions with overlap values ranging between 28.8% (May-June) and 96.3% (July-August) (Fig. 3a). These indicated 3.7 - 69.7% between-month dissimilarities in food compositions. High diet overlaps occurred in March-April, April-May, July-August, August-September and September-October whereas other pairwise monthly diet similarities revealed low overlaps ($S < 70\%$ in each case). The magnitude of variability in food composition was further attested by the average month-to-month overlap coefficient ($\bar{S} = 65.4\%$) which denotes a mean of 34.6% dissimilarity in month-to-month food compositions.

The overall extent of interseasonal diet overlap was high ($S = 90.7\%$), indicating that the fish was broadly consistent in its diet during the dry and wet seasons. This

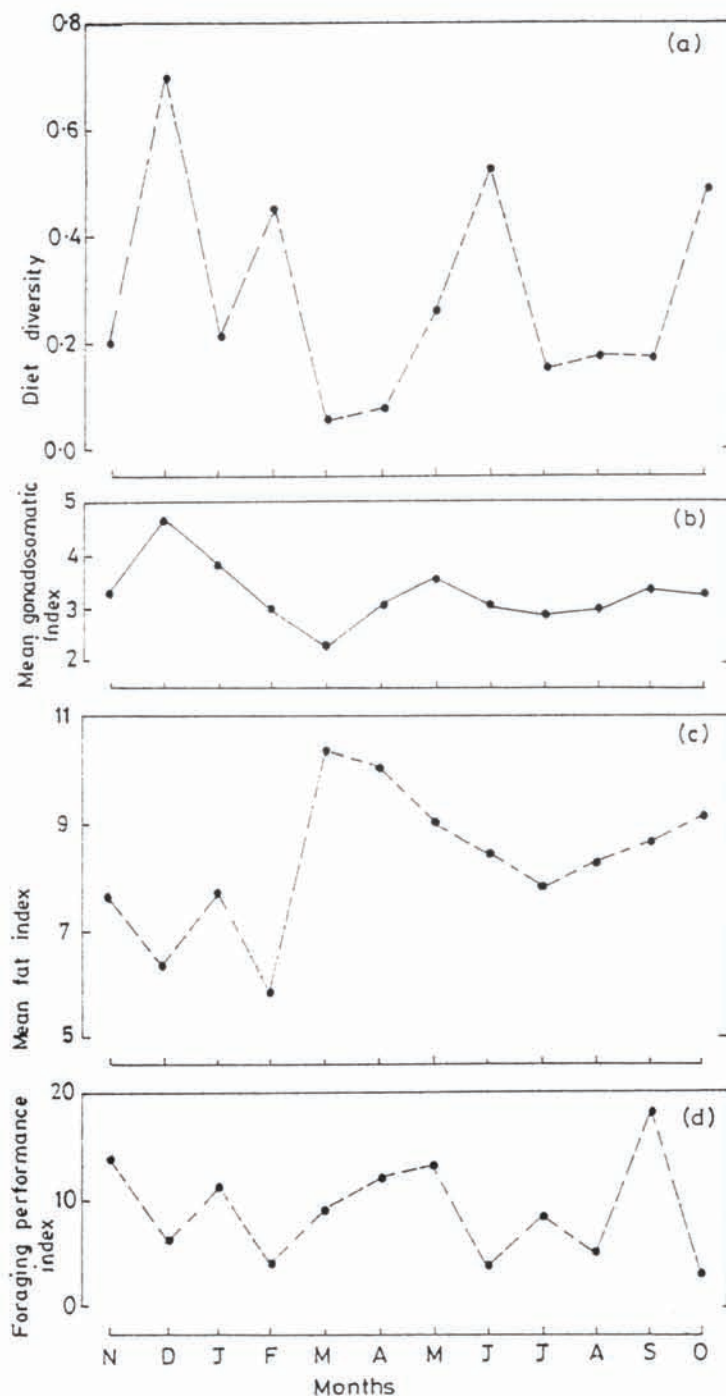


Fig. 2. - Monthly variation in diet diversity (a), female gonadosomatic index (b), fat index (c) and foraging performance index (d) of *Ilisha africana*.

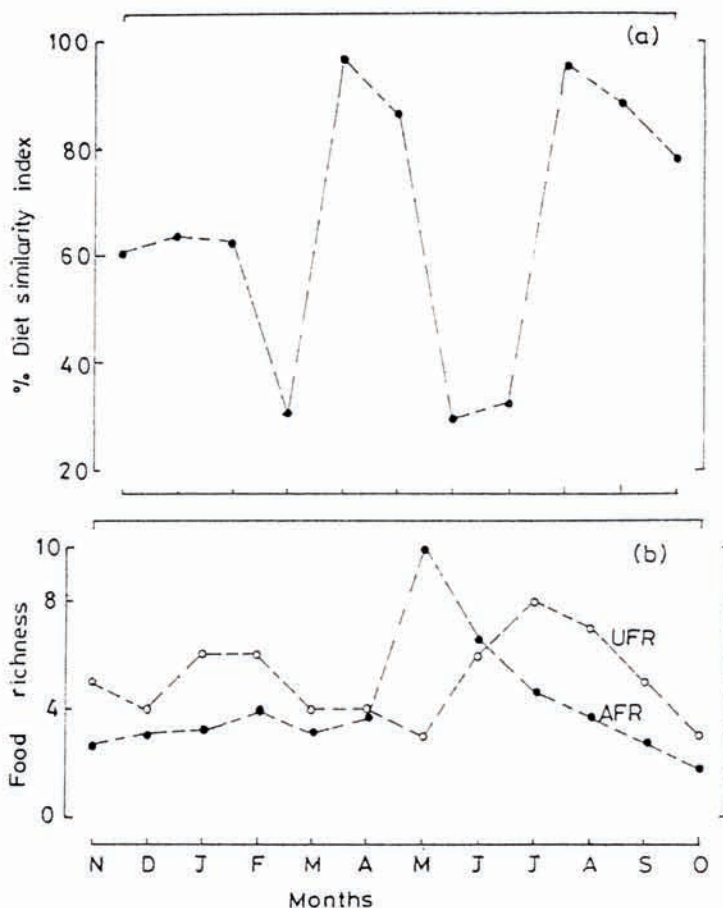


Fig. 3. - Monthly variation in % diet similarity index (a) and food richness (b) (UFR = unadjusted food richness; AFR = adjusted food richness) of *Ilisha africana*.

suggests that the short-term (month-to-month) variabilities in diet compositions were not strong enough to appreciably influence the long-term seasonal regimes; the latter tended to mask the month-to-month differences. The fish was more consistent in its wet season diet composition ($\bar{S} = 72.1\%$) than during the dry season ($\bar{S} = 61.7\%$).

Diet diversity

The gross low food richness (UFR = 10, AFR = 3.3) portrayed that *Ilisha africana* in Qua Iboe estuary had a highly restricted diet especially when viewed vis-a-vis the dietary lists given by Marcus (1982, 1986) for other locations in Nigeria. Monthly sequence in food richness indices (Fig. 3b) showed that UFR and AFR followed different patterns (Spearman rank correlation: $r_s = 0.355$, $P > 0.2$). The distribution of UFR was bimodal, with values ranging from 3 in May and October to 8 in July; the major peak was attained in July and minor one, in January-February. A bimodality also prevailed in the distributional pattern of AFR with values varying from 1.7 in October to 10.0 in May; the main peak was recorded in May and minor one, in February. Generally, the food

richness coefficients were higher during the wet season (UFR = 3 - 8; AFR = 2.7 - 10.0) than in the dry season (UFR = 4 - 6; AFR = 2.7 - 3.9).

The composite diet diversity index was low ($B_n = 0.110$) and represented only 11% of maximum possible diversity. This buttresses the earlier assertion that this species has a highly selective diet. Monthly trend in diet diversity was widely variable, with values of B_n ranging from 0.054 during the onset of the rains (March) to 0.701 during the onset of the dry season (November) (Fig. 2a); peaks were recorded in November, February, June and October. The dry season diet diversity ($B_n = 0.195 - 0.701$) appreciably exceeded that of the wet season ($B_n = 0.054 - 0.537$).

Monthly trends in female gonadosomatic index and diet diversity were closely related (Fig. 2a cf. Fig. 2b); mean GSI depicted three breeding peaks, the main one in the dry season (December) and minor ones in the wet season (May, September). Breeding activity was generally higher in the dry season than during the rains; this paralleled the seasonality regime in diet diversity. Reproductive investment thus broadly increased with diet diversity ($r_s = 0.632$, $P < 0.05$).

The relationship between fat index and diet diversity is presented in figures 2a and 2c. Mean FI had minimum and maximum values in February and March respectively; it was higher during the rains than in the dry season. This seasonality regime is the converse of the diet diversity pattern. Further evidence for this relationship is provided by the inverse correlation between both variables throughout the study period ($r = -0.700$, $df = 10$, $P < 0.02$). An exponential equation of the form:

$$FI = 6.3012 \left(\frac{1}{B_n^{0.1617}} \right) \quad (4)$$

accounted for 49% of the variation in fat index.

Foraging performance

The overall foraging performance index of *Ilisha africana* was quite low ($FP = 9.5$); monthly values ranged from 4.1 (February) to 17.7 (September) (Fig. 2d). Foraging performance remained low ($FP < 10$) in December, February-March, June-August and October while higher values ($FP \geq 10$) were recorded in November, January, April-May and September. There was an inverse relationship between foraging performance and diet diversity (Fig. 2a cf. Fig. 2d) ($r = -0.610$, $df = 10$, $P < 0.05$) according to the linear function:

$$B_n = 0.5449 - 0.0281 (FP) \quad (5)$$

which accounted for 37.2% of the variation in diet diversity. Foraging performance was slightly higher in the wet season ($FP = 3.4 - 17.7$) than during the dry season ($FP = 4.1 - 13.6$); this coincides with the seasonal trend in fat index. Fat index thus increased with foraging performance (Fig. 2a cf. Fig. 2d) ($r = 0.601$, $df = 10$, $P < 0.05$) according to an exponential equation of the form:

$$FI = 4.8014 (FP)^{0.2333} \quad (6)$$

which accounted for 36.2% of the variation in fat index.

DISCUSSION

The gross diet of *Ilisha africana* from Qua Iboe estuary comprised overwhelmingly, mysids and decapod crustaceans whereas each of the other items constituted < 5 % of the diet (Table I). The results indicate that the trophic status of this species can be assigned primarily to the carnivore guild. The decreasing rank-order of the composite food preference can be represented thus: mysids > decapods > fish eggs >

unidentified fish > amphipods > polychaetes, nematodes, clupeids, fish larvae, cephalopods. The food habit of *I. africana* in Qua Iboe estuary is broadly consistent with the findings of Fagade and Olaniyan (1973) in Lagos lagoon, Marcus (1982) off Brass and Bonny rivers and Marcus (1986) off the Lagos coast (Nigeria); the main difference is that the spectrum of items consumed by the population in Qua Iboe estuary is remarkably narrower than that reported for the fish off Brass and Lagos coast. The food habit of *I. africana* in Qua Iboe estuary can be described as oligophagous in view of the low food richness. The development of a low trophic spectrum is considered as a trait of the k-selected life history strategy (Bone and Marshall, 1982). This is expected for *I. africana* of the Qua Iboe estuary since it is known to incorporate both the r- and k-selection attributes in its reproductive strategy, the ecological significance of which is discussed by King (1991).

The restricted food habit of *Ilisha africana* was found to be maintained during the dry and wet seasons as reflected by the high interseasonal diet overlap. This consistency in diet composition suggests the establishment of well-defined food preference despite short-term (month-to-month) diet changes. This type of trophic specialization would profitably persist only where there is a stable environment that ensures year-round availability of specific food items. The ecological implication of this feeding strategy is discussed by Lowe-McConnell (1987) who stressed that extreme dietary specialization among the cichlids of the African great lakes could lead to stenophagy and the inability to alter feeding habits should environmental conditions change.

Most of the stomach contents of *Ilisha africana* portrayed vigorous reliance on pelagic foraging. Nevertheless, the ingestion of small amounts of sand and detritus provided a clue that it also foraged near the bottom. The stomach contents also depicted that this species fed largely on active prey which were presumably located visually and actively captured. This feeding habit is closely related to the morphology of the fish. *I. africana* has large eyes, laterally flattened body and deeply forked caudal fin; it is therefore capable of sustained high speed swimming which is necessary for foraging on active prey (see Paine *et al.*, 1982).

The high monthly incidence of fish eggs in the stomachs of *Ilisha africana* and their contribution to diet composition, suggest that they were not opportunistically consumed. Fish eggs in the diet seemed to be those of spawning conspecifics. This kind of filial cannibalism of the egg stage is also known to occur in *Prosopium coulteri* (Weisel *et al.*, 1973). Cannibalism on eggs can be linked to the spawning behaviour of *I. africana* which involves the congregation of females that broadcast eggs into open water where they are fertilized by milt simultaneously released by the males (King, 1991). Consequently, monthly trends in the relative importance of this item depicted a peak which coincided with maximum breeding activity in December; the year-round incidence of fish eggs in the diet also corresponded with the year-round breeding cycle of the fish (King, 1991). This general regime was corroborated by the fact that the dry season relative importance of fish eggs superseded (by a factor of ca. 5) that of the wet season, this being concurrent with the seasonality pattern in the breeding of the fish (King, 1991). Cannibalism on eggs and juveniles of *I. africana* was probably accentuated by the general depauperate food resources in the estuary since according to Nikolsky (1963), a decrease in the amount of food available to a fish population often exacerbates cannibalism.

The positive relationship between the dietary importance of mysids and fat index is similar to that between the dietary importance of chironomid larvae and fat index in haplochromine cichlids (Hoogerhoud *et al.*, 1983). It stresses the significance of mysids as energy source for *Ilisha africana*. The present study showed that high diet diversity was unimportant in the building up of fat reserves as depicted by the inverse correlation between both variables. However the positive relationship between gonadosomatic index and diet diversity showed that high diet diversity was associated with increased reproductive investment.

The present study revealed that *Ilisha africana* in Qua Iboe estuary consumed a wider array of items in the dry season than during the rains, in agreement with the finding of Marcus (1986) off the Lagos coast. This seasonality regime is analogous to that of the breeding cycle (King, 1991), the adaptive significance of which is explained by the role of high diet diversity in increased reproductive investment as noted above.

The observed temporal dynamics in diet composition, diet diversity and foraging performance of *Ilisha africana* may be dependent on the cycles of prey availability, abundance and encounter rates in the estuary (cf. Angermeier, 1982). Given the supposition that foraging efficiency and effort of *I. africana* remained constant throughout the year, the fluctuations in foraging performance can be considered as a crude index of the pulses in food resource availability and abundance. Since diet diversity is predictably responsive to resource variability (Angermeier, 1982), the inverse relationship between diet diversity and foraging performance of *I. africana*, depicted that the former expanded during periods of depressed resource availability and vice versa. A comparable regime between diet diversity and feeding rate has been established for the bird, *Parus gambeli* (Grundel, 1990). Angermeier (1982) who found similar trends in the foraging patterns of stream fishes, inferred that as food levels declined, the fishes consumed proportionally more of the relatively common prey-types. Based on this interpretation, it can be concluded that *I. africana* compensates for low food abundance and foraging performance by increasing diet diversity.

The current observation on the seasonality in diet diversity of *Ilisha africana* is supported by the optimal foraging theory (Schoener, 1971; Pyke *et al.*, 1977) which postulates an inverse relationship between diet diversity (diet breadth) and food resource abundance. In the tropics, evidence from fish dietary reports (e.g., Zaret and Rand, 1971; Welcomme, 1969, 1975, 1979; Lowe-McConnel, 1975; Angermeier and Karr, 1983) suggests higher wet season abundances of food resources and lower levels of abundances during the dry season. Therefore, fish diet diversity should expand in the dry season and contract during the rains in conformity with the optimal foraging theory. Assuming that the food resources of *I. africana* were more abundant during the rains (as reflected by the higher foraging performance index), the observed seasonal regime in diet diversity conforms with the optimal foraging theory. It can thus be inferred that food demand (indexed by foraging performance) is an important determinant of diet diversity; the fluctuations in foraging performance may therefore help regulate the prey-types to forage most profitably.

Since *Ilisha africana* in Qua Iboe estuary has a higher breeding activity in the dry season than during the rains, the decline in its foraging performance and diet consistency during the dry season is attributable to the priority in relative energy allocation to reproductive investment at the expense of active foraging. Conversely, increased wet season foraging performance and diet consistency may be adaptive as it ensures the building up of energy reserves prior to the dry season's breeding bout (see King, 1991). This is supported by the increased visceral fat deposition during the rains.

The present study has established that in *Ilisha africana*, increased foraging performance is necessary for the building up of fat reserves. Similar relationships between feeding activity and amount of visceral fat reserves have been reported for other fishes (Nikolsky, 1963; Olatunde, 1978).

Acknowledgements. - I wish to thank Mr. A.O. Okon (ex Department of Zoology and Fisheries, University of Cross River State, Uyo, Nigeria) for field and laboratory assistance.

REFERENCES

- ANGERMEIER P.L., 1982. - Resource seasonality and fish diets in an Illinois stream. *Env. Biol. Fish.*, 7(3): 251-264.

- ANGERMEIER P.L., 1985. - Spatio-temporal patterns of foraging success for fishes in an Illinois stream. *Am. Midl. Nat.*, 114(2): 342-359.
- ANGERMEIER P.L. & J.R. KARR, 1983. - Fish communities along environment gradients in a system of tropical streams. *Env. Biol. Fish.*, 9: 117-135.
- BAGENAL T.B., 1978. - Aspects of fish fecundity, pp. 75-101. In: *Ecology of freshwater Fish Production* (Gerking S.D., ed.) Blackwell Scientific Pub.
- BONE Q. & N.B. MARSHALL, 1982. - Biology of fishes. 253 pp. Blackie and Son Ltd.
- DAJOZ R., 1977. - Introduction to Ecology (Translated by A. South). 416 pp. Hodder and Stoughton Education.
- FAGADE S.O. & C.I.O. OLANIYAN, 1973. - The food and feeding interrelationship of the fishes in Lagos lagoon. *J. Fish Biol.*, 5: 205-225.
- GRUNDEL R., 1990. - The role of dietary diversity, prey capture sequence and individuality in prey selection by parent mountain chickadees (*Parus gambeli*). *J. Anim. Ecol.*, 59: 959-976.
- HOOGERHOUD R.J.C., WITTE F. & C.D.N. BAREL, 1983. - The ecological differentiation of two closely resembling *Haplochromis* species from Lake Victoria (*H. iris* and *H. hiatus*; Pisces, Cichlidae). *Neth. J. Zool.*, 33(3): 283-305.
- HYSLOP E.J., 1980. - Stomach content analyses: a review of methods and their application. *J. Fish Biol.*, 17: 411-429.
- KING R.P., 1989. - Distribution, abundance, size and feeding habits of *Brienomyrus brachyistius* (Gill, 1862) (Teleostei: Mormyridae) in a Nigerian rainforest stream. *Cybiurn*, 13(1): 25-36.
- KING R.P., 1991. - Some aspects of the reproductive strategy of *Ilisha africana* (Bloch, 1795) (Teleostei, Clupeidae) in Qua Iboe estuary, Nigeria. *Cybiurn*, 15(3): 239-257.
- KING R.P., UDOIDIONG O.M., EGWALI E.C. & N.A. NKANTA, 1991. - Some aspects of the trophic biology of *Ilisha africana* (Teleostei; Pristigasteridae) in Qua Iboe estuary, Nigeria. *J. afr. Zool.*, 105: 261-274.
- LOWE-McCONNELL R.H., 1975. - Fish Communities in tropical Freshwater: their Distribution, Ecology and Evolution. 337 pp. Longman, London.
- LOWE-McCONNELL R.H., 1987. - Ecological Studies in tropical Fish Communities. 382 pp. Cambridge Univ. Press.
- MARCUS O., 1982. - The biology of the clupeid, *Ilisha africana* (Bloch) off the Nigerian coast. Ph.D Thesis, Univ. Lagos, Nigeria.
- MARCUS O., 1986. - Food and feeding habits of *Ilisha africana* (Bloch) (Pisces: Clupeidae) off the Lagos coast, Nigeria. *J. Fish Biol.*, 29: 671-683.
- MOSS B. & J.W. EATON, 1966. - The estimation of numbers and pigment content in epipelagic algae populations. *Limnol. Oceanogr.*, 11: 584-595.
- NIKOLSKY G.V., 1963. - The Ecology of Fishes. 352 pp. Academic Press Inc. (London) Ltd.
- ODUM E.P., 1971. - Fundamentals of Ecology. 574 pp. W.B. Saunders Company.
- OLADIMEJI A.A., 1987. - Impacts of oil pollution on Nigerian fishing industry. *Nig. J. appl. Fish Hydrobiol.*, 2: 81-90.
- OLATUNDE A.A., 1978. - The food and feeding habits of *Eutropius niloticus* (Ruppell) family Schilbeidae (Osteichthyes: Siluriformes) in Lake Kainji, Nigeria. *Hydrobiologia*, 57(3): 197-207.
- PAINE M.D., DODSON J.J. & G. POWER, 1982. - Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. *Can. J. Zool.*, 60: 1635-1641.
- PYKE G.H., POLLIAM H.R. & E.L. CHARNOV, 1977. - Optimal foraging: a selective review of theory and tests. *Quart. Rev. Biol.*, 52: 137-154.
- SCHOENER T.W., 1971. - Theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, 2: 369-404.
- WEISEL G.F., HANZEL D.A. & R.L. NEWELL, 1973. - The pygmy whitefish, *Prosopium coulteri*, in western Montana. *Fish. Bull.*, 71(2): 589-596.
- WELCOMME R.L., 1969. - The biology and ecology of the fishes of a small tropical stream. *J. Zool., London.*, 158: 485-529.
- WELCOMME R.L., 1975. - The fisheries ecology of African floodplains. *CIFA Techn. Pap.*, 3: 1-51.
- WELCOMME R.L., 1979. - Fisheries Ecology of Floodplain Rivers. 317 pp. Longman Group Ltd., London.
- WOOTTON R.J., 1973. - The effect of size of food ration on egg production in the female three spined-stickleback *Gasterosteus aculeatus* L. *J. Fish Biol.*, 5: 89-96.
- ZARET T.M. & A.S. RAND, 1971. - Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology*, 52: 336-342.

Reçu le 23.09.1992.

Accepté pour publication le 07.05.1993.